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Die-back of *Phragmites australis*: influence on the distribution and rate of sediment methanogenesis

BRIAN K. SORRELL*, HANS BRIX, HANS-HENRIK SCHIERUP & BENT LORENZEN

*Department of Plant Ecology, Institute of Biological Sciences, University of Aarhus, Denmark (*author for correspondence, present address: National Institute of Water and Atmospheric Research, P.O. Box 8602, Christchurch, New Zealand)*

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Abstract. Methanogenesis was measured during the summer of 1994, in sediment cores and bulk samples from a *Phragmites australis* wetland in northern Jutland, Denmark. We compared sediment from healthy reed and dying-back reed, and an open lagoon resulting from die-back. Cores revealed variability with depth and between sites, with the highest rates coinciding with layers of organic gyttja, and negligible methane production from the underlying sand base. Methanogenesis rates in the lagoon and die back sites were higher (up to 100–150 nmol h^{-1} g^{-1} dry wt. sediment) than in the healthy reed (50–80 nmol h^{-1} g^{-1}), with the highest rates being recorded from May to July. At these times, methanogenesis was markedly temperature-limited; samples incubated at 30 °C a non-limiting temperature, gave rates as high as 200–400 nmol h^{-1} g^{-1} for the lagoon and die-back areas and 150 nmol h^{-1} g^{-1} for the healthy area. Addition of 8 mM acetate and H_2/CO_2 headspace suggested that both acetate-fermenting and CO_2-reducing bacteria were present. Acetate additions suggested some co-limitation by substrate availability, with acetate limitation occurring in the healthy site during July and in the die-back site during August. Lower rates during August, especially in the healthy area, were associated with low water levels which resulted in more oxidized sediments. The data reveal highly variable methanogenesis in the sediment which, when considered with sediment depths, indicates that sites of *Phragmites* die-back have significantly greater rates of anaerobic mineralization than surrounding healthy wetland, and may be intense sources of methane.

Introduction

Shallow wetlands dominated by emergent aquatic plants are amongst the most productive of all plant communities, since they receive ample light, water and nutrients (Jones 1986). Dense plant growths can profoundly influence soil chemistry and nutrient cycling, due to both the growth processes of the plants and the large amount of organic carbon they represent (Reddy et al. 1989; Boon & Sorrell 1991). These processes may affect sediment development that in turn affects plant growth, through alteration of sediment oxygen demand and accumulation of toxic organic compounds. However, relatively little is known about the impact of emergent plants on carbon cycling in freshwater sediments.

Methanogenesis is a key process for understanding feedback effects between plants and decomposition processes in sediments. It is normally the only quantitatively significant pathway for anaerobic carbon mineralization in freshwater wetlands, since concentrations of alternative electron acceptors, such as nitrate and sulphate, are generally too low to support large populations of nitrifying or sulphate-reducing bacteria. It is obligately anaerobic, and therefore liable to be influenced by the effects of plants on sediment redox potential. Plants may increase sediment redox due to their root oxygen release and transpiration (Dacey & Howes 1984; Armstrong et al. 1992), or decrease it with the additional organic matter they provide (Whiting et al. 1986). Surprisingly few studies have addressed differences in methanogenesis between comparable vegetated and unvegetated sediments (Boon & Sorrell 1991).

The decomposition processes in wetlands are also related to their trace gas emissions into the atmosphere. Freshwater wetlands may account for 25 to 40% of global methane emissions (Bartlett & Harriss 1993), and an understanding of their methanogenic processes is therefore also relevant to increasing tropospheric methane concentrations. Recent fluctuations in the rate of methane increase and consequent uncertainty about the global sinks and sources driving atmospheric methane levels (Khalil & Rasmussen 1993) further stress the need for a better understanding of sediment methane production. Vegetated wetlands are particularly complex and difficult to understand, due to the many feedback effects between plants and bacteria and the additional transport pathways plants provide (Chanton & Dacey 1991; Sorrell & Boon 1994).

The common reed, *Phragmites australis* (Cav.) Trin. ex Steud., is one of the most widespread of emergent plants and one of the most productive. Its roots can penetrate deeply into sediments, and it is known to affect some biogeochemical processes (Hansen & Andersen 1981). Reed has extremely efficient internal gas transport which can rapidly transfer gas between the atmosphere and sediment, and provides high root oxygen release (Armstrong et al. 1992). On the other hand, its development often accumulates sufficient organic carbon to stimulate reducing conditions and hence reduce growth and cause senescence. In some parts of Europe, anthropogenic eutrophication is accelerating this process and causing extensive reed die-back (Čižková-Končalovă et al. 1992). For these reasons, sediment biogeochemistry in reed communities and how it is affected by die-back are particularly relevant for understanding interactions between plants and sediment methanogenesis.

This study examines sediment methanogenesis in three distinct zones of a reed wetland in northern Jutland, Denmark, viz. healthy reed growth, dying-back reed, and open water resulting from die-back. The spatial and temporal variation in methanogenesis is examined from samples collected during the

1994 summer, and related to temperature, substrate availability and sediment characteristics. We then combine the methanogenesis rates with information on sediment depths to evaluate the gross methane production in the wetland.

Materials and methods

Study area

The Vejlerne Nature Reserve in northern Jutland, Denmark (57°05′N, 9°04′E) is a 150 km^2 freshwater wetland, created during the 1870s by the construction of dykes across the mouths of two shallow saltwater fjords. There are extensive monospecific stands of reed, in which small unvegetated lagoons sometimes occur, where older reed material has died back. These lagoons are occasional pockets within the younger, healthy reed. We sampled in Han Vejle in the eastern fjord, comparing methanogenesis in sediments taken from (i) healthy reed growth; (ii) dying-back reed adjacent to lagoons; and (iii) unvegetated lagoons. During summer, shoot density in the healthy reed is > 200 m^2, and shoot height is 1.5–2 m. In the dying-back zone, a more reducing sediment develops, due to organic matter accumulation, and the rhizomes die from the tips, fill with water, and sink through the sediment to the underlying sand base. Death of rhizomes is accompanied by death of the shoots, which become sparser and shorter before disappearing completely. No living reed material remains in the lagoons; the dead rhizomes, having sunk through the sediment, are buried under ca. 0.3 m of organic gyttja and 0.1 m overlying swampwater.

Sediment sampling

Sediment samples were collected on four occasions during the 1994 summer (14.4.94; 16.5.94; 7.7.94; 31.8.94). The weather was cool and wet in the early part of the study, followed by a six-week warm, dry period and ending with more rain in late August (Figure 1). A time lag between rainfall and its effect on the water level in the wetland produced high levels early in the study and lower levels later.

To estimate the spatial variability within the three sites, five sediment cores were collected randomly from each on 7.7.94. The cores were taken with a stainless steel corer (12 cm diameter, 155 cm length) with sharpened teeth for cutting through the rhizome mat. Cores were extruded with a plunger and a 60 ml sample of each visible horizon from each core immediately removed and sealed in gas-tight 100 ml bottles containing nitrogen gas. These were returned to the laboratory within 6 h and stored for 12 h at the

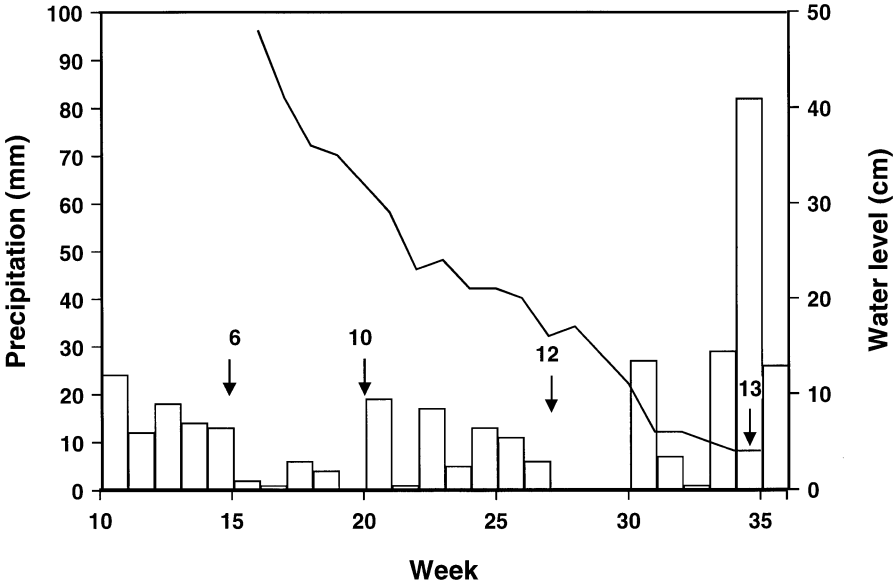

Figure 1. Weekly precipitation (bars) and water level (line) at Vejlerne during the summer 1994 study period, plus the *in situ* sediment temperature (°C) on the collection dates (arrows). Precipitation and water level data courtesy Aage V. Jensen Foundation.

in situ temperature (12 °C), before being prepared for methanogenesis. Due to the high spatial variability revealed (see results), sediment for all other measurements was collected from each site in bulk and pooled in 10 l sealed plastic buckets to reduce variation. The large volumes of sediment, high redox capacity and negligible headspace in the buckets ensured that the sediment remained anaerobic. The buckets were stored for at least 48 h at the *in situ* temperature before measurements, to allow the sediment to recover from any oxidation during collection. Preliminary tests showed that the methanogenic activity of sediment stored this way remained unchanged for at least 4 weeks, and all measurements were made within this time.

Sediment properties

Five additional cores were taken from each site and sediment samples (11) were stored in sealed containers. Water content was determined after drying at 105 °C for 24 h and loss on ignition after combustion in a muffle oven at 500 °C for 6 h. In addition, organic carbon was analyzed titrimetrically after wet combustion of dried sediment in $H_2SO_4/K_2Cr_2O_7$. The redox capacity of the sediment was measured with brightened platinum electrodes and calomel reference electrodes as described by Schierup & Jensen (1981).

Methanogenesis

60 ml samples were withdrawn from the buckets with plastic syringes and transferred to 100 ml glass bottles which were immediately placed in a nitrogen-purged glove bag. Once placed in the nitrogen atmosphere, the flasks received 4 ml of a de-oxygenated cysteine solution (final concentration = 0.03%). They were then gassed with nitrogen for 2 min to remove all pre-existing methane, which can cause errors in methanogenesis analyses (Kiene & Capone 1986), and sealed with plastic caps fitted with teflon-lined septa, which had been tested beforehand and found not to store or release significant methane quantities. Samples of the headspace were immediately withdrawn for time zero analyses, using 2 ml gas-tight glass syringes, and the flasks then incubated in a temperature-controlled water bath in the dark. Further headspace samples were removed during the following 24–48 h. Time courses of methane concentration were not linear during the first 1–3 hours, presumably because of equilibration processes, after which slopes were linear for at least 30 h. Rates were therefore routinely estimated from headspace samples taken between 3.5–20 h. Headspace samples were analyzed on a Shimadzu Model GC-8A Gas Chromatograph using a flame ionization detector (100 °C), nitrogen carrier gas (50 ml l^{-1}) and a Porapak T column (50 °C). The gas chromatograph was calibrated immediately before and after each set of analyses with 1000 ppmv methane standards in nitrogen (Mikrolab, Aarhus, Denmark). Concentrations were corrected for methane dissolved in the sediment (Smith & Baresi 1989), although this error was small, and rates calculated from the slope of the methane-time plot and headspace volume. Rates were calculated on both volumetric and dry weight bases; dry weights were obtained after drying the samples at 120 °C for 24 h.

For each collection, methanogenesis was measured at the *in situ* temperature and at 30 °C, a non-limiting temperature for methanogenesis in these sediments, and in the absence and presence of acetate (final concentration = 8 mM), the main substrate for methanogenesis in freshwater sediments. Preliminary experiments established that 8 mM acetate and 30 °C saturated methanogenesis in the Vejlerne sediment. To test further for substrate limitation, we added both acetate and 20%H_2/80%CO_2 in the gas phase to some samples, to identify both acetate-fermenting and CO_2-reducing bacteria.

Statistics

Differences between sites, seasonal differences, and effects of temperature and substrate additions were all tested by Analysis of Variance (ANOVA). The data were tested for heterogeneity of variances before analysis with Cochran's *C* test. No heterogeneity was detected in the pooled sediment,

Table 1. Depth zones (cm) for the sediment horizons in the healthy, die-back and lagoon areas of the reed wetland. Cores taken during July 1994.

Horizon	healthy	die-back	lagoon
a: mixed plant detritus and sediment	0–30	0–20	–
b: dense black gyttja	30–40	20–35	0–30
c: mixed sand and plant detritus	40–70	35–60	–
d: sand	> 70	> 60	> 30

but samples from the cores were heterogeneous and skewed lognormally. This was corrected by logarithmic transformation. Means for the transformed data were calculated as described by Parkin et al. (1990), and confidence limits by Land's (1971) method for exact confidence limits, which gives the best estimate for lognormal data (Parkin et al. 1990). A range of orthogonal and nested ANOVAs were used, depending on the experimental designs. Differences between individual means were then determined with Student-Newman-Keuls tests. Significance was always tested at $P < 0.05$ unless noted otherwise.

Results

Sediment methanogenesis profiles

Methanogenesis profiles in the sediment are shown in Figure 2. Cores from the healthy site revealed four distinct layers (Table 1). It is evident that the basal sand had almost no methanogenic activity whilst rates in the other layers were higher (up to 30–50 nmol g^{-1} h^{-1}). The mixed sand and detritus layer was poorly defined in the die-back site and hence pooled with the basal sand. Cores from this area show that methanogenesis was highest in the gyttja layer and again virtually zero in the sand base. The unvegetated lagoon had only two horizons, the basal sand and an 0.3 m-deep layer of overlying gyttja with dead plant material. The sand base again had very low activity, whereas rates in the overlying mud were up to 100 nmol g^{-1} h^{-1}.

The methanogenic profiles were extremely variable with depth in the die-back and healthy sites, especially the latter, due to the variability of the depth and thickness of the organic layer. A two-way orthogonal ANOVA (site*horizon) was possible with the logarithmically transformed data, which conformed to normality and homogeneity of variance prerequisites . Both site and horizon effects were significant ($P < 0.01$), although there were no significant interactions between these. The highest rates were in those horizons which contained more organic sediment rather than sand or plant debris,

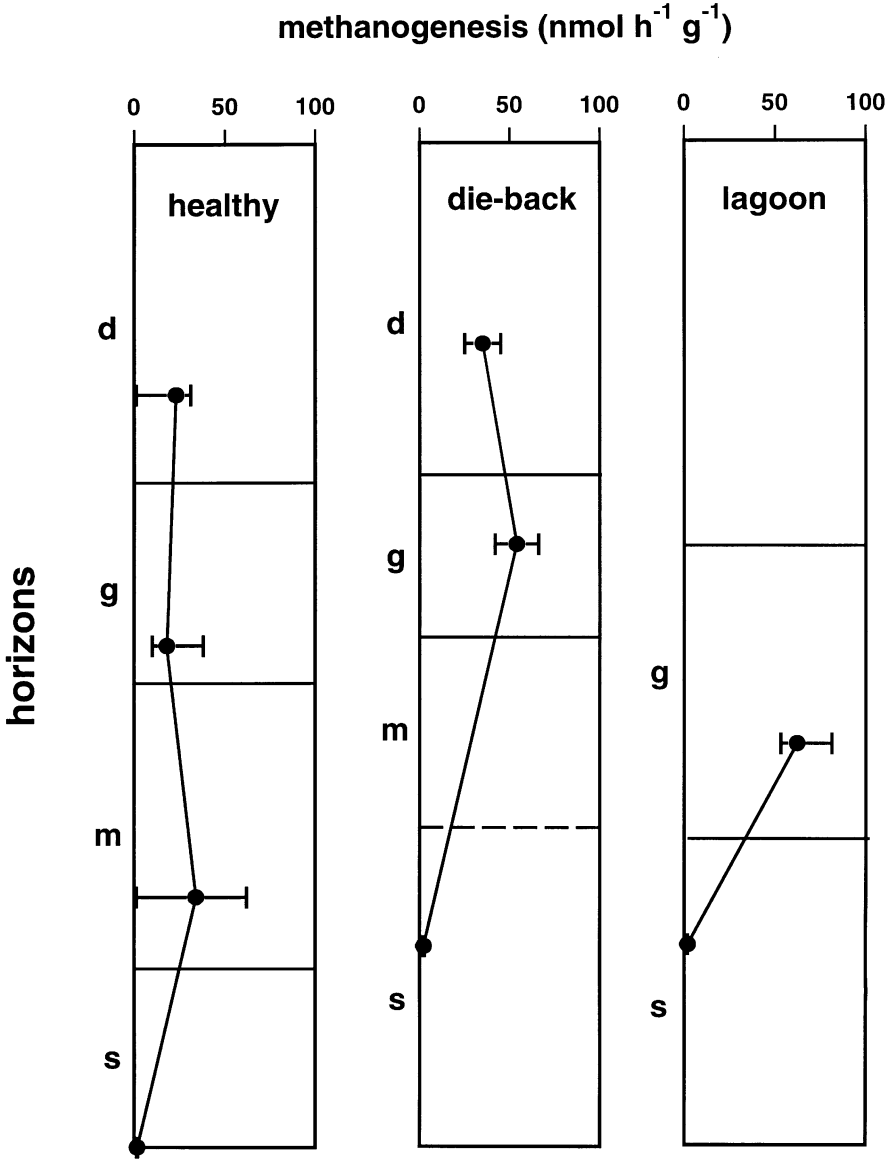

Figure 2. Vertical profiles of methanogenesis in sediment horizons from cores in the three sites collected on 7 July 1994 (sediment temperature 12 °C). Means with 95% confidence limits calculated by Land's (1971) exact method for lognormal means. Approximate depths of horizons are shown schematically for (d) superficial detritus of compressed plant debris and sediment, (g) dense organic gyttja, (m) mixed sand and plant debris, and (s) sand base.

Table 2. Properties of the organic gyttja horizons in the healthy, die-back and lagoon areas, measured during August 1994 (mean values ± SD, n = 5).

	Healthy	Die-back	Lagoon
Loss on ignition (%DW)	21.7 ± 7.8	18.8 ± 4.6	41.8 ± 1.9
Organic carbon (%DW)	10.1 ± 3.3	10.0 ± 1.2	14.1 ± 1.1
Water content (%)	85.1 ± 5.9	92.9 ± 4.3	95.6 ± 0.4
Redox capacity (meq g^{-1}DW)	0.52 ± 0.07	0.89 ± 0.31	1.10 ± 0.03

methanogenesis in the most active gyttja did not differ between lagoon and die-back sediments ($P = 0.15$), but was significantly lower in the healthy site ($P < 0.01$). The core data gives an indication of the high spatial variability in methanogenesis in reed sediments. Sediment used in the remaining experiments was collected in bulk and pooled to reduce the variation.

Temperature limitation

Rates of methanogenesis during the summer and their temperature-dependence are shown in Figure 3. The pattern for the three sites was similar, with relatively low rates in April, higher rates in May and July, and very much lower in August, despite a high *in situ* temperature. A two-way orthogonal ANOVA (temperature*site) showed that increasing temperature had little effect in April, when the number of bacteria was probably lower, but that sediments from all sites were markedly temperature-limited in May and July. The lagoon and die-back sites remained temperature-limited in August, but there was no measurable methane production from the healthy site at either temperature. The lower rates in August are most likely due to the low water levels in the wetland (Figure 1), which would improve drainage through the sediment. Analyses of the active gyttja layers (Table 2) showed that organic matter and carbon contents were high in all sites, but that water content was lower in the healthy reed than in the other areas. Sediment from the healthy reed also had a lower redox capacity in August, and had visibly changed from black (reduced) to brown (oxidized). Rates in the lagoon and die-back sites were similar, but were always significantly higher than in the healthy site. Rates at 30 °C showed similar relative differences, except that the die-back site was extremely temperature-limited in July.

Substrate limitation

Microbial processes in nature are rarely limited by a single factor, and there was also evidence for some substrate (acetate) co-limitation of methanogenesis in these sediments together with the temperature limitation (Figure 4).

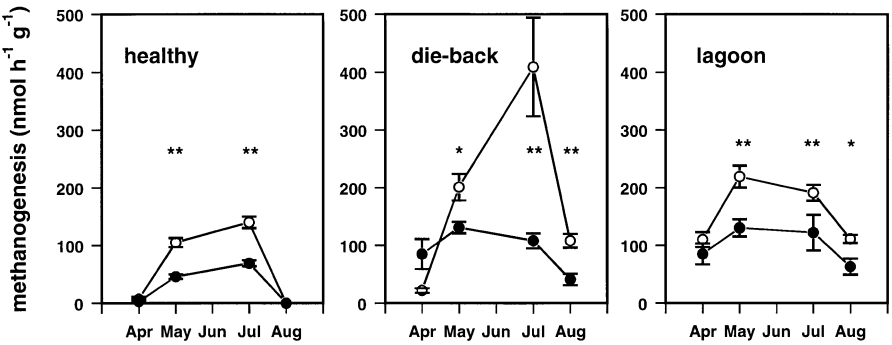

Figure 3. Temporal variation of sediment methanogenesis during the 1994 summer for the three sites, at the *in situ* temperature (●) and at 30 °C (○). Mean values ± SD, n = 5. Sediments showing significant differences between the two temperatures are indicated by * ($P < 0.05$) and ** ($P < 0.01$).

Effects of substrates were readily detected in these experiments, as the control samples were the same pooled sediment as that used in the temperature experiments, which had low variability (c.v. < 0.1). Acetate limitation was more equivocal during the study than temperature, but a three-way nested ANOVA (temperature*site*±acetate within time) showed that the lagoon and healthy sites were acetate-limited in July as was the die-back site in August. Sediment at 30 °C also showed acetate-limitation in May and July, though not in August. The lack of a consistently greater acetate limitation at 30 °C than at the *in situ* temperature shows that limitation of methanogenesis in these sediments is not a simple temperature vs. substrate interaction. Other factors such as microbial numbers and other nutrients must be involved.

Addition of acetate and H_2CO_2 to the lagoon sediments showed that both acetate fermenters and CO_2 reducers were present (Figure 5). A two-way nested ANOVA (substrate*temperature within time) showed that added substrates were usually more effective at 30 °C than at the in situ temperature, especially in April and August, when other factors were limiting (see previous section). The greater stimulation at 30 °C suggests that temperature limitation was largely responsible for the smaller response at the *in situ* temperature. The effect of adding both substrates together was usually not additive, indicating that competition for other nutrients can also be limiting. In July, however, very high rates resulted from addition of both substrates provided that the temperature was not limiting, suggesting greater nutrient availability.

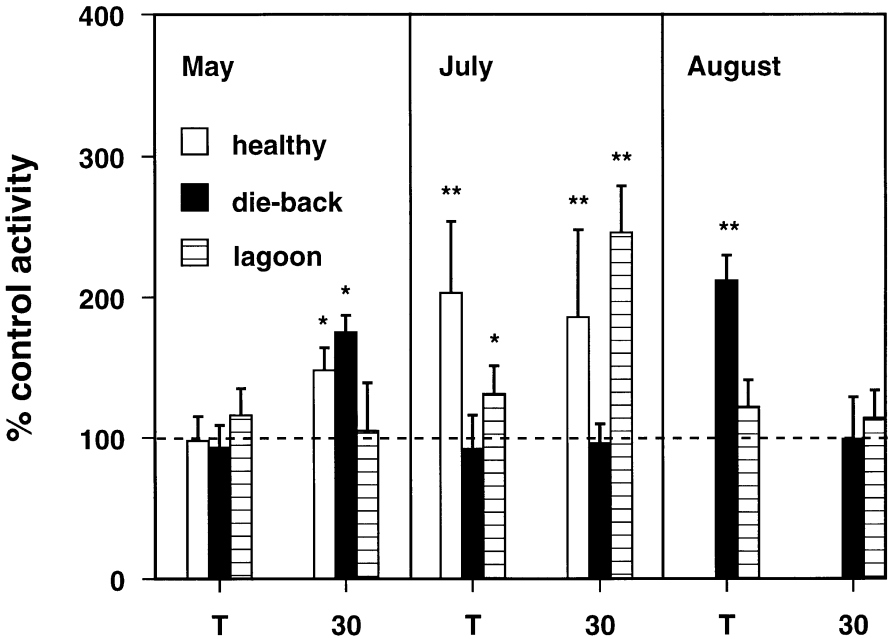

Figure 4. Effect of added acetate (8 mM) on methanogenesis in sediments from the three sites as % of the control activity (dashed line) at the *in situ* temperature and at 30 °C. Error bars are 1 SD (n = 5). Treatments giving significant responses are indicated by * ($P < 0.05$) and ** ($P < 0.01$)

Gross methane production

Total methanogenesis in the three sediments were estimated from data of the peak midsummer period (May–July) by combining the measured *in vitro* rates, when expressed per unit volume, with the sediment depths observed in the cores. On this basis, the total production during summer ranged from 1–7 mmolCH_4 m^{-2} day^{-1} in the healthy reed, 10–25 mmolCH_4 m^{-2} day^{-1} in the die-back site, and 45–53 mmolCH_4 m^{-2} day^{-1} in the lagoon. These ranges result from both the volumetric methanogenesis rates, which are significantly different between sites (higher in the lagoon and die-back sites and lower in the healthy reed), and the thickness of the sediment layers, especially the highly active gyttja, which accumulates in the lagoons. The very low methanogenesis rates in the healthy site at the beginning and end of the study (Figure 3) suggest that its gross production may be even lower on an annual basis.

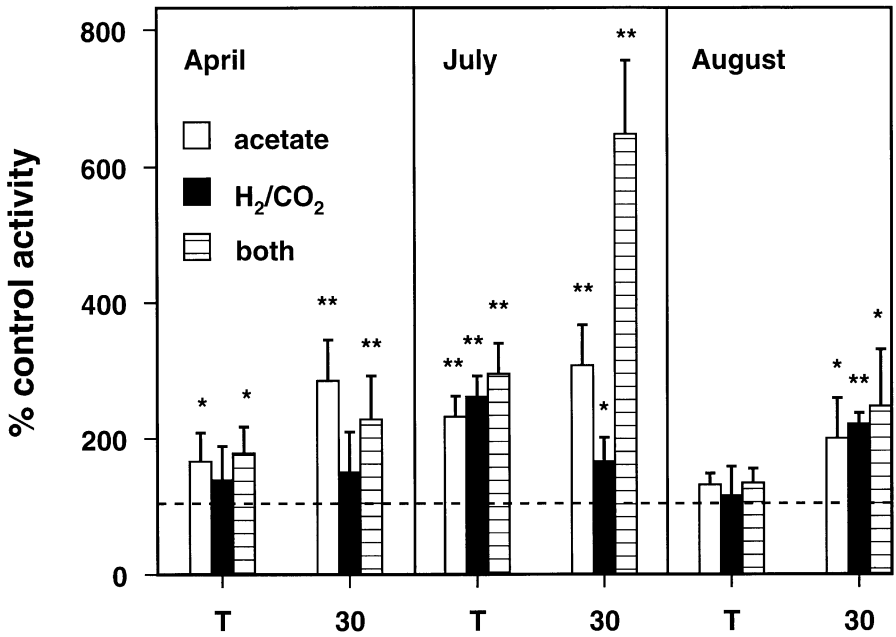

Figure 5. Effect of acetate and H_2/CO_2 additions on lagoon sediment as % of the control activity (dashed line) at the *in situ* temperature and at 30 °C. Error bars are 1 SD (n = 5). Treatments giving significant responses are indicated by * ($P < 0.05$) and ** ($P < 0.01$).

Discussion

In this study we have shown that methane production in reed-dominated wetlands is highly variable, with rates differing between various depth horizons, over time, and especially spatially as the reed ages and dies. Sediments under healthy reed are more oxidized than in die-back and lagoon sites (Table 2), so their lower methanogenesis rates are unsurprising, and the thinness of the methanogenic horizons in the healthy sites further reduces their methane production per unit area. Measurements of gross methane production in wetland sediments remain relatively scarce, especially with respect to spatial variation, but frequently show the high variations with depth we observed. Rates also differ greatly depending on sediment type, season and latitude. Our rates for the gyttja layers in the healthy reed in Vejlerne are somewhat higher than those of fen sediments from a fringing reed band in another Danish wetland (ca. 30 nmol h^{-1} g^{-1} at 24 °C, Priemé 1994), and the highest rates we found in our lagoon and die-back sites are more similar to those for peat sediments in spruce wetlands in the Appalachians (Yavitt & Lang 1990) and a warm, shallow wetland in Australia (Boon & Sorrell 1991). They are, however, considerably lower than rates measured in sub-tropical Everglades

marl (Bachoon & Jones 1992) or warm Italian rice fields (Holzapfel-Pschorn et al. 1985).

Such comparisons between sites must also include longer-term changes. Our data suggest that the progress and balance of a reed wetland between healthy and dieback states is important for its methane production, and by implication, emission to the atmosphere. Whilst we measured methane production, not emission, the two are usually well-correlated. Wetlands are generally viewed as sites of high methane production (Bartlett & Harriss 1994), but the spatial variability may be considerable and production related to the development and aging of the population. In general, methane emissions from wetlands increase as their primary productivity increases (Whiting and Chanton 1993), but substantial variability is usually seen in these analyses (e.g. Figure 1 of Whiting and Chanton 1993). Our study suggests one explanation for such variability – the change in emissions as the vegetation develops and senesces. Reed wetlands may not necessarily produce and release great amounts of methane whilst they are healthy and actively growing, but become more intense methane producers when they senesce and die. This die-back production occurs in small areas in a reed wetland such as the Vejlerne population studied here. Little is known about the progression of these natural die-back patterns, but vegetation analyses suggest that the die-back lagoons can subsequently be colonized by *Typha latifolia* L., which is more tolerant of reducing conditions. Alternatively, reed may itself re-colonize if continued decomposition of the gyttja eventually allows the sediment to become less reducing. The time course of these changes and how they affect methane production remains unknown. Understanding of carbon cycling and methane production is of particular importance for reed, for it is one of the most widespread of all wetland plants and forms large monospecific stands in many parts of the world. The die-back of reed wetlands in central and eastern Europe has recently aroused great concern, due to their economic and environmental significance, and because the die-back is clearly anthropogenic (Čižková-Končalová et al. 1992). The results of our study suggest an additional concern, in that anthropogenic die-back will cause a period of more anaerobic decomposition and greater methane production.

This suggestion ought, however, to be viewed cautiously. Although the correlation between total methane production and release in wetlands is undeniable, the two are not always closely linked in time or space, and emissions are generally more dynamic and variable than methanogenesis. There are several possible fates for methane produced in saturated sediments: it can be oxidized in unsaturated zones, at the sediment surface or in the overlying water, or in the rhizosphere (Epp & Chanton 1993). Alternatively, it may escape to the surface via ebullition and hence escape oxidation, especially

in unvegetated sites (Keller & Stallard 1994), or be rapidly transported to the atmosphere through the plants (Chanton & Dacey 1991; Sorrell & Boon 1994). It cannot therefore be assumed that the higher methanogenesis we observed in the die-back and lagoon sites will necessarily result in greater emissions from these areas. The standing water over the lagoon and die-back sediments offers a possible habitat for methane oxidizing bacteria, whilst the more effective internal gas transport in the reed in the healthy site could allow a greater proportion of the methane produced there to escape to the atmosphere. The presence of vascular plants in methanogenic sediments leads to higher rates of release than from comparable adjacent sediments without plants (Chanton et al. 1989; Sorrell & Boon 1994). Reed has particularly high rates of internal gas transport, associated with a pressurized gas flow (Armstrong & Armstrong 1991; Brix et al. 1992), and these gas flows provide much higher methane releases through plants than gas transport by diffusion alone (Sorrell & Boon 1994; Chanton et al. 1993). All of these factors could bias emissions toward the healthy reed rather than the die-back sites.

On the other hand, the more oxidized healthy reed sediment is likely to have a greater population of methane-oxidizing bacteria as well as fewer methanogens. The highly oxidized rhizosphere adjacent to plant roots can be an important site of methane oxidation (Epp & Chanton 1993). These factors agree with decomposition in healthy reed being more aerobic than in the dying-back sites, especially if the elevation is great enough to allow intermittent drying-out as occurred during August in our study. In studies of methane emissions from temporary wetlands with partially-saturated soils, variations in soil moisture content are normally the most important factor correlating with both production and emission (Bubier et al. 1993; Nilsson & Bohlin 1993). Lower water contents allow sediments to change from sites of methane production to consumption, greatly reducing their annual methane release. This moisture-dependence is also evident in our study, where the die-back and lagoon sites remained saturated and reducing in August, whilst the healthy site was more oxidized. Methanogens cannot survive in such oxidized sediments, but their presence may be very dynamic, since only a few hours, or at most days, are required after flooding for sediments to become reducing enough for methanogenesis (Gambrell et al. 1991). In Vejlerne, these patterns probably vary from year to year. The 1994 summer was relatively dry, whereas the healthy reed could remain waterlogged in wetter years.

Whilst moisture content may be the most important factor controlling methanogenesis in such partially and intermittently wetted soils, it is high and constant and hence less important in permanently flooded wetlands and lake sediments. In these sites, temperature and organic matter inputs are more important. Methanogenesis tends to adjust for and become controlled

by organic carbon accumulation in the long term (Kelly & Chynoweth 1981; Yavitt & Lang 1990), but can also show instantaneous or short-term temperature limitation (Schutz et al. 1990; Dunfield et al. 1993). The reed sediments from Vejlerne are consistent with these concepts, especially in the permanently waterlogged lagoon and die-back areas. Their methanogenesis increased only slightly during the season as temperature increased, yet were highly temperature limited when given an instantaneous temperature increase. The changing effectiveness of temperature increases and substrate additions during the season also suggest that competition between the acetate-fermenting and CO_2-reducing bacteria may be dynamic and competitive, despite the relatively constant releases. However, whilst substrate additions are useful for demonstrating that methanogenesis is substrate limited, they do not unequivocally discriminate between acetate fermenters and CO_2 reducers, especially when CO_2 rather than hydrogen is limiting the CO_2 reducers (Davidson & Schimel 1995). Isotope studies of the contributions of CO_2 and acetate to methanogenesis (e.g. Rothfuss & Conrad 1993) would be necessary to confirm this.

Our estimation of the methanogenesis by the Vejlerne sediments has nevertheless revealed the importance of die-back for accelerating production. Die-back sites showed much higher methanogenesis per sediment volume, thicker layers of the most active methanogenic horizons, and remained waterlogged and productive during dry periods when the healthy marsh became drained and inactive. This suggests the presence of small, highly productive point sources in wetlands with natural die-back patterns, such as Vejlerne. The shift towards a more reducing, methanogenic wetland caused by the extensive anthropogenic die-back of reed could therefore be an important factor increasing methane production from wetlands.

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